Occurrence of Prolonged Diapause in Ethmiid Moths

(Lepidoptera: Gelechioidea)

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Diapause in its broadest sense, an arrested state of growth and development, has been studied from many standpoints. Attempts have been made to explain causes of its initiation and termination and to more precisely define, predict and classify the various kinds. One aspect that seems to have been slighted is prolonged diapause, the maintenance of a dormant state for more than one year. Yet, this must be an important evolutionary strategy in insects, where so many kinds are dependent for food and shelter upon the inconstant occurrence of specific organisms. Not only must insects cope with extremely variable factors in the physical environment, such as seasonal changes in Temperate Zones, but many species must display a precise timing with their hosts as well, whether they be plants or other insects.

Thus it is not surprising that in a diversity of insects the arrest in development has been shown to sometimes last more than a year. Examples are known in eggs of Orthoptera (Kreasky, 1960; Rentz, 1973); prepupal larvae of gall midges (Barnes, 1952), sawflies (Prebble, 1941; Sullivan & Wallace, 1967), and anthophorid bees (MacSwain, 1958); in pupae of various moths and butterflies; and in adults of chrysomelid beetles (Ushatinskaya, 1967).

Prolonged diapause usually is expressed by a small fraction of a one-season diapausing population (e.g., Dohanion, 1942; Ushatinskaya, 1967). It seems to be an expression of genetic heterogeneity, and the few late individuals emerge synchronously with their normal season but more than one year later. Most researchers have not been sufficiently fascinated with the phenomenon to invest years for the chance of meager results. Thus experimental data are lacking to show whether some kind of fixed polyphenic expression of the genotype is involved as a kind of natural buffer against extraordinary extremes or whether dormant individuals are responding to suboptimal conditions, or whether an interaction between genetic heterogeneity and variable microenvironmental factors is the cause.

Some insects, by contrast, in exploiting marginal and extreme conditions seem to have evolved prolonged diapause to cope with typically irregular seasonal and/or biotic conditions. In such examples whole

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populations may undergo dormancy for more than one year as in certain high elevation grasshoppers (Kreasky, 1960) and yucca moths (Powell, 1973a, unpublished data). A distinction needs to be made between the two classes of prolonged diapause, but experimental studies with yucca moths indicate that the distinction may lie in the degree of fitness to the optimum in environmental conditions rather than in clear cut classes of insect species.

Most of the literature on this phenomenon for Lepidoptera is limited to chance rearings in situations remote from natural populations. Usually successful emergence has not been recorded beyond the third year, although there are a few reports of longer duration, up to 6–7 years in Lasiocampidae and Geometridae (Standfuss, 1896) and 8 years in *Rothschildia* (Saturniidae) (Rowley, 1923). By contrast, more detailed studies in other insects indicate prolonged diapause is not limited to chance situations occasioned by highly unnatural conditions. For example, Barnes (1943, 1952) showed that larvae of gall midges pass up to 10–12 winters in diapause and that the modality of longevity varies from one year's collection to another; while Prebble (1941) found that diprionids remain in dormancy 1–6 years with the number of years variable in different parts of the geographic distribution.

In Microlepidoptera prolonged diapause is known in Tortricidae and in prodoxine Incurvariidae, the yucca moths. Dohanion (1942) found that 5% of prepupal larvae of *Melissopus* (Laspeyresiini) overwintered 3 years, and the Douglas-fir cone moth, *Barbara* (Eucosmini), is reported by Keen (1958) to undergo dormancy lasting 3 years. Hedlin (1960a, b) indicates that a large proportion of *Barbara* pupae remain in diapause during some years. In yucca and agave moths of the genera *Prodoxus* and *Agavenema*, prepupal larvae wait in the dry inflorescence stalks commonly up to 4 years, and successful emergence has been obtained after 8 years (Powell, 1973a, unpublished data).

Thus the ability to delay for protracted periods occurs among scattered moth taxa, and although it has not been demonstrated for many Gelechioidea, I have previously speculated that facultative delay of 2 or more seasons may be a widespread means by which Ethmiidae cope with seasonal drought (Powell, 1973b: 40). This idea was based on an early report that emergence after 1 and 2 winters had been obtained in a European species of *Ethmia* (deJoannis, 1926), and on the fact that up to the time of my writing (December, 1970) I had observed living pupae of 3 species of this genus that had been in diapause for 16 months or more. During the subsequent 3 years a few adults of 2 of these species have continued to emerge (Table 1), tending to confirm my speculation.

Table 1. Number of moths emerging following storage of pupae through winter in various situations: R = Russell Reserve shed; U = Unheated room; L = Lab (mobile trailer) with fluctuating temperature above 18°C.

Winter:	(prior to)	1969–70	1970–71	1971–72	1972–73
Housing:	L	R	U	R	R/L
scylla	–	0	2	1	2/–
semilugens	3	0	0	2	0/1

The data are given here, as enumeration of such observations is a necessary step to more detailed analysis of prolonged diapause. The general biologies of the 2 species and details on the particular collections (lot JAP 69D60 for *Ethmia scylla* and 69E78-79 for *E. semilugens*) have been recorded elsewhere (Powell, 1971).

ETHMIA SCYLLA Powell

This univoltine, diurnal species is known only from the inner Coast Range in central California. Larvae collected in April, 1969, were provided with small blocks of dry yucca stalk pith, owing to the widespread habit of members of this genus to bore into soft woody substrates for pupation. The yucca blocks were stored in a translucent, plastic box in an open-sided shed at the U. C. Russell Biological Reserve in inland Contra Costa County, California, from August, 1969, to the end of February, 1970. This place has been used for several years to expose overwintering Microlepidoptera from various parts of California to greater winter extremes than available at coastal Berkeley.[1] The Russell Reserve is located about 85 airline km northwest of the *scylla* collection site and has comparable winter conditions. However, no *scylla* adults emerged in 1970, which is difficult to explain, particularly because at the same time a collection of a closely related species, *E. plagiobothrae* Powell (lot 69D58, see Powell, 1971) taken on the same day in April, 1969, at a site 7 km west of the *scylla* colony, was housed in the same conditions and all individuals successfully emerged in February, 1970.

The following year some of the *scylla* pupae were taken for study and description (Powell, 1971), and while I was away on sabbatic leave the remainder of the collection was stored in an unheated room at Walnut Creek, Contra Costa County. Temperature and humidity conditions were

[1] Temperature and humidity data at the shed will be summarized in a study of prolonged diapause in yucca moths, in preparation.

not monitored but certainly were much more uniform than at the Russell Reserve shed. Nonetheless, two individuals (1 ♂, 1 ♀) emerged between September, 1970, and August, 1971. The box was again housed at the Russell shed during the 1971–72 and 1972–73 winters, from October to April. The lot was watered at the end of March and was transferred to a mobile trailer lab at Berkeley with natural lighting conditions during spring and summer months. One male eclosed in March, 1972, and in late February, 1973, the final 2 *scylla* (♂ ♂) emerged, after 45 months in diapause. At least these later emergences occurred within the natural flight period, late February to early April (Powell, 1973b).

Subsequent examination of the pupation substrate revealed that no pupae remained unhatched. Unfortunately, in addition to 3 pupae harvested in 1970 and the 5 moths that successfully emerged, 8 more individuals pupated and developed but on eclosion were trapped in the emergence tackways (Powell, 1971: 17), possibly by fungal sealing of the outer silken caps. Thus additional completion of diapause occurred during one or more years, possibly including 1970, after one year dormancy. All development took place in a translucent container in shallow galleries a few mm into the porous yucca pith, so photoperiod as well as other factors could have been involved in diapause break.

ETHMIA SEMILUGENS (Zeller)

This nocturnal species is widespread in the southwestern Nearctic in desert-margin habitats and other arid places. Based on collection records of adults and my rearing data, I concluded that the species is facultatively doubled brooded, presumably in response to rainfall because the known hosts are 2 species of annual *Phacelia* (Powell, 1971, 1973b). Overwintering is accomplished by pupae, and most flight records are for March and April. Resulting progeny then either complete development and emerge in July, August or September or remain in diapause.

Larvae collected in Inyo County, California, in May, 1969, were allowed to pupate in folds of soft paper toweling. Three moths completed development during 1969 under laboratory conditions, the first emergence occurring in July, after about 6 weeks pupation. Subsequent housing for the remainder of the collection was similar to that described for *E. scylla*. Cocoons of *semilugens* in several translucent containers (plastic vials and polyethylene bags) were placed at Russell Reserve during the 1969–70 winter, and no moths matured in the spring. Part of the lot was harvested for study of the pupae in late 1970 (Powell, 1971), and the remainder were housed at Walnut Creek during the 1970–71 winter, which also produced no emergence. Overwintering in

1971–72 was the same as for *scylla*, and the cocoons were watered on March 30, then transferred to Berkeley on April 10; 30 days later 2 adults (1 ♂, 1 ♀) emerged. For the 1972–73 winter the collection was divided, part going to the Russell shed and part remaining at the trailer lab in Berkeley, under natural lighting, fluctuating temperature above 18°C, and essentially dry conditions. No more individuals completed development in the Russell shed segregate, but in Berkeley 1 female emerged in September, 1973, after 52 months in diapause.

Examination of the pupation substrate in October, 1973, showed that in addition to 2 pupae that died in immature stages and 3 moths proceeding through development in 1969, 3 pupae harvested for study in 1970, and 3 which matured to adults in 1972–73, 2 other pupae remained in unopened cocoons, possibly still living.

The emergence of 2 moths in 1972, 40 days following artificial watering, after 33 months dormancy, suggests that sporadic rainfall in desert situations may be a critical factor in breaking diapause.

LITERATURE CITED

BARNES, H. F. 1943. Studies of fluctuations of insect populations X. Prolonged larval life and delayed subsequent emergence of the adult gall midge. J. Anim. Ecol., 12: 137–138.

BARNES, H. F. 1952. Studies of fluctuations of insect populations XII. Further evidence of prolonged larval life in the wheat blossom midges. Ann. Appl. Biol., 39: 370–373.

DOHANION, S. M. 1942. Variability of diapause in *Melissopus latiferreanus*. J. Econ. Entomol., 35: 406–408.

HEDLIN, A. F. 1960a. Diapause in the Douglas-fir cone moth, *Barabara colfaxiana* (Kft.). Canad. Dept. Agric., Div. Forest Biol., Bi-Mon. Progr. Rept., 16(6): 4.

HEDLIN, A. F. 1960b. On the life history of the Douglas-fir cone moth, *Barbara colfaxiana* (Kft.) (Lepidoptera: Olethreutidae), and one of its parasites *Glypta evetriae* Cush. (Hymenoptera: Ichneumonidae). Canad. Entomol., 92: 826–834.

DE JOANNIS, J. 1926. Longévité chez *Ethmia* (*Psecadia*) *decemguttella* Hb. Bull. Soc. Entomol. France, 1926: 151.

KEEN, F. P. 1958. Cone and seed insects of western forest trees. U.S. Dept. Agric., Tech. Bull., 1169; vi + 168 pp.

KREASKY, J. B. 1960. Extended diapause in eggs of high-altitude species of grasshoppers, and a note on food-preferences of *Melanoplus bruneri*. Ann. Entomol. Soc. Amer., 53: 436–438.

MACSWAIN, J. W. 1958. Longevity of some anthophorid bee larvae (Hymenoptera: Apoidea). Pan-Pacific Entomol., 34: 40.

POWELL, J. A. 1971. Biological studies on moths of the genus *Ethmia* in California (Gelechioidea). J. Lepid. Soc., 25, suppl. 3, 68 pp.

POWELL, J. A. 1973a. Facultative longevity and polyphenism in diapause of

yucca moths. Presented at 24th annual meeting of The Lepidopterists' Society, Sarasota, Fla., June 22, 1973.

POWELL, J. A. 1973b. A systematic monograph of New World ethmiid moths (Lepidoptera: Gelechioidea). Smithson. Contr. Zool., 120; 302 pp.

PREBBLE, M. L. 1941. The diapause and related phenomena in *Gilpinia polytoma* (Hartig). V. Diapause in relation to epidemiology. Canad. J. Res., D, 19: 437–454.

RENTZ, D. C. 1973. The shield-backed katydids of the genus *Idiostatus*. Mem. Amer. Entomol. Soc., 29; 211 pp.

ROWLEY, R. R. 1923. Extended pupal duration. Canad. Entomol., 55: 198.

STANDFUSS, M. 1896. Handbuch der Palaarktischen Gross-Schmetterlinge fur Forscher und Sammler. Second ed. Fischer; Jena, Germany [not seen].

SULLIVAN, C. R. AND D. R. WALLACE. 1967. Interaction of temperature and photoperiod in the induction of prolonged diapause in *Neodiprion sertifer*. Canad. Entomol., 99: 834–850.

USHATINSKAYA, R. S. 1967. The extended diapause of the Colorado beetle (*Leptinotarsa decemlineata* Say) and the conditions for its occurrence. Rev. Appl. Entomol., 55: 112 [abstract].